SEED PRODUCTION AND SEED PREDATION IN *GENTIANA NEWBERRYI* (GENTIANACEAE) POPULATIONS

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Abstract

In the Sierra Nevada, flowers of *Gentiana newberryi* Gray were significantly larger and produced more ovules at Little Valley (2000 m) and Forestdale Divide (2580 m) than at Frog Lakes (3120 m). The mean number of seeds produced at Little Valley was significantly larger. Predation reduced seed set at the higher elevation sites. Herbivores removed 37.9% of the flowers at Frog Lakes. Predispersal seed predators (Diptera larvae) consumed all of the seeds in 64.3% of the capsules at Forestdale Divide and 3.0% at Frog Lakes. Later blooming flowers experienced less predation but risked permanent snow cover before the seeds matured.

Successful reproduction in plants is influenced by availability of resources (Stephenson 1981; Evenson 1983; McDade and Davidar 1984; Harder et al. 1985; Stanton et al. 1986; Primack 1987; Horvitz and Schemske 1988; Primack and Kang 1989) and pollinators (Levin and Anderson 1970; Bierzychudek 1981; Thomson 1981; Pleasants 1983; Waser 1983; Motten 1986; Galen and Newport 1988; Ashman and Stanton 1991) and the ability to avoid predation (Louda 1982a, b, 1983; Crawley 1988). Factors affecting seed set may vary from year to year and among populations (Douglas 1981; Campbell 1987). In areas where resources and pollinators are unpredictable, a successful perennial plant should be able to set seeds or produce seedlings under a variety of limitations (Sutherland 1986). While self-fertilized (Levin 1971; Jain 1976; Barrett 1988; Karoly 1992) and vegetatively produced plants (Evenson 1983; Waller 1988) increase the number of genetically identical plants in the population and can increase the risk of inbreeding depression, those plants that are successful may have coadapted genes that are advantageous for the current environmental stresses experienced by the population (Lloyd 1979; Waser and Price 1983; Barrett 1988).

Flower removal by herbivores and predispersal seed predators can limit the number of seeds produced by a population (Janzen 1971; Arnold 1982; Louda 1982a, b; 1983; Crawley 1988; Hendrix 1988). The rates of herbivory and seed predation in a species have been found to vary between sites and along a climatic gradient (Louda 1982a, 1983).

Gentiana newberryi Gray is restricted to high elevation wet meadows in eastern California, western Nevada, and southern Oregon (Hickman 1993). A perennial, *G. newberryi* has protandrous funnel shaped flowers with corollas that are usually white with greenish spots (Munz 1973). In the White Mountains, California (3550 m elevation), *Gentiana newberryi* is visited by *Bombus sylvicola* Kirby, *Bombus balteatus* Dahlbom, *Bombus huntii* Greene, and *Bombus morrisoni* Cresson (Spira 1983; Spira and Pollak 1986). Flowers under insect exclosures in the White Mountains did not produce mature fruits or seeds (Spira 1983; Spira and Pollak 1986) but *G. newberryi* in Little Valley, Nevada did produce viable seeds (Barnes and Rust 1994). When flowers under exclosures in Little Valley were supplemented with pollen from a flower on the same plant, there was no difference in the number of seeds produced when compared with cross-pollinated flowers (Barnes and Rust 1994). Spira (1983) found 2.9–3.6 vegetative rosettes per plant in the White Mountains. In Little Valley 90% of ramets observed had at least one lateral rhizome. Spira (1983) and Spira and Pollak (1986) observed marmots and noctuid moth larvae consuming *G. newberryi* flowers but not fruits or seeds. Predispersal capsule predation of *Gentiana saponaria* L. by *Endothenia habesana* Walker (Lepidoptera) larvae has been observed to reduce seed set by 94% (Windus 1990).

We investigated the differences in seed set per flower in three populations of *Gentiana newberryi* at different elevations in the Sierra Nevada. We measured soil water potential and recorded pollinator visits to determine if limitations influencing seed set were similar at each site. Flowers were examined for evidence of herbivory or capsule predation.

Methods and Materials

Study sites. In July 1992, three study sites were established in flat montane meadows before flowering and were followed weekly until snowfall covered the areas. These sites were located along the eastern edge of the Sierra Nevada escarpment at elevations from 2000 to 3120 m. The Little Valley site (119°52'W, 39°15'N) in Washoe Co., Nevada is located in the Whittell Forest and Wildlife Area owned by the University of Nevada, Reno (elev. 2000 m). The Forestdale Divide site (119°58'W, 38°40'N) in Alpine Co., California is located in the Toiyabe National Forest (2580 m). The Frog Lakes site (119°17'W, 38°3'N) is in the Hoover Wilderness area of the Toiyabe National Forest in Mono Co., California (3120 m). All three meadow sites are covered by snow during the winter and collect and retain water from snow melt longer than surrounding areas. This study was conducted during the sixth year of a drought (James 1992). Snowfall was about 50% of normal and melted earlier than usual from all three sites (James 1992).

Seed production. Each week, at each site, 10–20 *G. newberryi* flowers that had newly opened corollas and dehiscing anthers were marked and numbered. Flower phenology was observed and each marked flower was checked weekly for signs of herbivore damage. When capsules matured (usually 3–4 weeks after flower opening), the flowers were removed and stored in individual waxed paper bags. The number of mature seeds and undeveloped ovules in each capsule was counted. The female reproductive potential for *G. newberryi* flowers at each site was estimated by calculating the mean number of mature seeds produced by the marked flowers. The total number of ovules produced and the percentage of ovules that produced mature seeds were also determined. After counting, the mature seeds from each flower were placed in individual waxed paper bags and stored outdoors. Capsules with Diptera larvae were placed in individual clear plastic vials with air holes for overwintering and rearing.

Mature seeds from three to four randomly chosen flowers at each site were used to estimate germination potential. Thirty to fifty seeds from each flower were placed in a separate petri dish on brown paper over kimpack moistened with a 400 ppm gibberellic acid solution. The seeds were kept at 15°C for 7 days and then alternated between 15°C for 12 hr and 25°C for 12 hr for 14 days. The percentage of seeds germinated at each site was calculated.

Flower predation. All collected *G. newberryi* capsules were checked for evidence of capsule predators. Capsules that contained insect-damaged seeds were examined to determine if any intact mature seeds remained.

Marked flowers were examined for any evidence of herbivore damage. If flower tags were missing or no longer attached to a flower then the flower was assumed to have been removed by an herbivore. The sites were monitored weekly for the presence of herbivores that could potentially consume *G. newberryi*.

Floral characteristics and pollinators. Corolla length and maximum corolla tube width of *G. newberryi* flowers were measured during the second week in August in several areas of each site. A flower size index was developed by multiplying corolla length by corolla tube width. Nectar volume was measured at each site using capillary tubes. The soil moisture potential was measured with a Quickdraw Series 2900 Soil Moisture Probe where the flowers were measured.

Bees or other potential pollinators were rarely observed at the Forestdale Divide or Frog Lakes sites, so all visits were recorded. At Little Valley, hourly transects were walked twice each week and all flower visits by bees were recorded (Barnes and Rust 1994). Beginning in September, when bees were rare at Little Valley, all

TABLE 1.   COMPARISON OF *GENTIANA NEWBERRYI* FLOWER SIZE AT THREE SITES IN THE SIERRA NEVADA DURING THE SECOND WEEK OF AUGUST 1992. Values are means ± standard deviation. [1] Index developed by multiplying corolla length by maximum corolla width to compare sites. [2] Bonferroni t-tests, means with the same letter are not significantly different (P < 0.05).

Site	Corolla length (mm)	Corolla width (mm)	Flower size index[1]	n	Bon- Grp[2]
Little Valley	40.7 ± 5.6	12.7 ± 3.1	530.4 ± 188.2	50	A
Forestdale Divide	38.3 ± 3.7	13.0 ± 2.0	495.1 ± 68.5	16	A
Frog Lakes	25.8 ± 4.1	7.0 ± 2.2	187.2 ± 90.3	25	B

observed insect visits to flowers were recorded. Samples of all insect visitors at each site were collected for identification by R. Rust, University of Nevada, Reno and R. Brooks, University of Kansas, Lawrence.

Statistical analyses. Analysis of variance (GLM in SAS 1990) was used for all comparative analyses within and between populations. Arcsine transformations were used for analysis of percentage data and other cases which violated assumptions. When analysis of variance indicated a significant difference, a Bonferroni t-test was used for pairwise comparisons within and between populations. Linear regression (SAS 1990) was used to determine if there was a relationship between soil moisture and flower size at each site.

RESULTS

Floral characteristics and pollinators. Flowering of *G. newberryi* began during the first week in July at Little Valley and the first week in August in Forestdale Divide and Frog Lakes and continued until the second week in October at all three sites. *Gentiana newberryi* corollas at Little Valley and Forestdale Divide were similar in size but the corollas at Frog Lakes were significantly smaller (F = 45.01, df = 2,88, P < 0.0001) (Table 1). Linear regression showed a significant relationship between soil moisture and corolla size in Little Valley (F = 117.78, df = 1,48, P < 0.0001) with the larger flowers found in wetter soil (Table 2). The regression of flower size and soil moisture was not significant at Forestdale Divide (F = 1.02, df = 1,14, P = 0.3309) or Frog Lakes (F = 2.22, df = 1,23, P = 0.1500) (Table 2).

Nectar was available in most *G. newberryi* flowers at each site throughout the study. The mean amounts of nectar available (mm/1 lambda capillary tube) per flower at Little Valley (23.0 ± 13.2 (SD)), Forestdale Divide (25.4 ± 16.1), and Frog Lakes (6.6 ± 3.7) were not significantly different (F = 0.06, df = 2,12, P = 0.0627).

Table 2. Within Site Comparisons of Soil Water Potential and *Gentiana newberryi* Flower Size at Three Study Sites in the Sierra Nevada during the Second Week of August 1992. Flower size index values are means ± standard deviation. [1] Index developed by multiplying corolla length by maximum corolla width. [2] Bonferroni t-tests comparing flower size within each site. Means with the same letter are not significantly different (p < 0.05).

Site	Soil water potential (KPa)	Flower size index[1]	n	Within site BonGrp[2]
Little Valley	0	764.1 ± 79.0	10	A
	4	617.6 ± 106.8	10	B
	8	557.7 ± 106.0	10	B
	18	425.1 ± 102.3	10	C
	35	287.5 ± 74.4	10	D
Forestdale Divide	0	508.6 ± 72.6	6	A
	9	512.8 ± 23.0	5	A
	15	460.4 ± 97.3	5	A
Frog Lakes	0	140.6 ± 33.9	5	A
	6	141.2 ± 27.8	5	A
	10	221.5 ± 120.2	10	A
	19	210.8 ± 74.1	5	A

Bombus vosnesenskii Radoszkowski, *B. edwardsii* Cresson, *Anthophora bomboides* Kirby, *A. urbana* Cresson, *A. terminalis* Cresson, and *Apis mellifera* L. were the most common visitors to *G. newberryi* in Little Valley. The frequency of bee visits decreased rapidly from the onset of flowering in early July. Only one bee was seen after August even though there were *G. newberryi* flowers with nectar and pollen available until early October. In September, one *B. edwardsii* was observed visiting *G. newberryi* at Forestdale Divide. Small syrphid flies, *Eupeodes volucris* Osten Sacken, were the only other visitors observed at this site. A total of ten visits by *B. vosnesenskii* and *B. edwardsii* were observed over two months at Frog Lakes. Bumble bees were rare in the Sierra Nevada in 1992, compared to most years (R. Rust and R. Thorp personal communication). *Bombus edwardsii, B. vosnesenskii,* and *Bombus appositus* Cresson were observed throughout the day in Little Valley in 1991 from August 1 through September 27 (Barnes and Rust 1994) but few were seen in 1992. *Gentiana newberryi* flowers close at night and open the following morning. Therefore, flowers were not monitored for nocturnal pollinator activity.

Seed production. The mean number of ovules per flower at Little Valley (232.0 ± 94.7, n = 82) and Forestdale Divide (186.7 ± 68.6, n = 12) was significantly higher than at Frog Lakes (118.2 ± 72.5, n = 10) (F = 7.76, df = 2,101, P = 0.0007). The mean number of

mature seeds produced per capsule in all marked flowers was significantly higher in Little Valley (131.6 ± 112.9, n = 84) than at Forestdale Divide (10.3 ± 33.3, n = 97) or Frog Lakes (13.8 ± 44.2, n = 68) (F = 76.02, df = 2,246, P < 0.0001). There was no significant difference in the percent of seeds that germinated at Little Valley (84.8% ± 11.1%), Forestdale Divide (46.8% ± 33.1%) or Frog Lakes (59.4% ± 31.5%) (F = 2.11, df = 2,8, P = 0.1840).

Floral predation. Predation by mammalian flower herbivores and/or insect predators of capsules was found at Forestdale Divide and Frog Lakes but not at Little Valley. When marked flowers that were damaged or removed by predators are excluded from the analysis, the mean number of mature seeds produced per capsule is significantly higher at Little Valley (131.6 ± 112.9, n = 84) than at Forestdale Divide (41.5 ± 57.2, n = 24) or Frog Lakes (39.1 ± 68.2) (F = 13.24, df = 2,129, P < 0.0001).

Capsules containing Diptera larvae or with all seeds damaged occurred in 64.3% of all capsules at Forestdale Divide and in 3.0% at Frog Lakes. All seeds within the capsule were eaten before pupation. The number of seeds produced per capsule in marked flowers was significantly reduced by Diptera larvae at Forestdale Divide (F = 12.29, df = 1,119, P = 0.0006) but not at Frog Lakes (F = 0.03, df = 1,48, P = 0.8749).

No mammalian herbivore damage to *G. newberryi* plants or flowers was observed at Forestdale Divide. At Frog Lakes 37.9% of marked flowers were removed by mammalian herbivores. The reduction in the number of mature seeds produced per marked flower was not significant (F = 3.35, df = 1,90, P = 0.0704). During week four (September 5), only five intact flowers were found on the study site and many corolla tubes were found on the ground. No herbivores were ever observed foraging on *G. newberryi,* but many flowers on the ground had the base of the corolla tube missing. During week five (September 12), many more flowers were present and of 20 marked only one was removed by herbivores. These marked flowers produced significantly more seeds per capsule than flowers marked in previous weeks (F = 4.82, df = 2,63, P = 0.0112).

Common potential herbivores observed in the area were yellow bellied marmots (*Marmota flaviventris*), pikas (*Ochotona princeps*), Belding's ground squirrel (*Citellus beldingi*), and alpine chipmunks (*Eutamius alpinus*).

DISCUSSION

The flower size and number of ovules produced per *G. newberryi* flower were not significantly different between Little Valley (2000 m) and Forestdale Divide (2580 m). The flowers at Frog Lakes (3120 m) were smaller and had fewer ovules. This suggests that ovule

number may be related to flower size. High elevation plants and flower size are frequently limited by cold temperatures and desiccating winds (Billings and Mooney 1968, Bliss 1971, Douglas 1981) and a shorter snow free growing season. They are often smaller than the same species at lower elevations. Size variation in *G. newberryi* is correlated with altitude and moisture (Hickman 1993). Little Valley had more variation in flower size and soil water potential suggesting that soil water was an important limiting resource at this site but not at the higher elevation sites.

There is no significant difference in the percentage of ovules that produce mature seeds at the three sites if only seed capsules with some mature seeds are considered. This excludes aborted seed capsules and herbivore damaged capsules. Predation by flower herbivores at Frog Lakes and Diptera larvae at Forestdale Divide are responsible for the large difference in the number of mature seeds produced. Nearly 65% of the seed capsules at Forestdale Divide and 3% at Frog Lakes had all seeds damaged. More capsules aborted or were unable to mature seeds due to early snowfall at the higher elevation sites than at Little Valley.

A significant reduction in seed set due to insect damage to seeds has been observed in other species of *Gentiana* (Windus 1990). However, no seed capsule predators were reported on *G. newberryi* in the White Mountains, California (3550 m) (Spira 1983, Spira and Pollak 1986). It is not apparent why the Diptera larvae are frequently found at two higher elevation sites at Forestdale Divide (2580 m) and Frog Lakes (3120 m) and not at Little Valley (2000 m) or the White Mountains. Louda (1982a) found predispersal seed predator numbers decreased over a climatic gradient from the coast to the mountains in *Haplopappus squarrosus* Hook. & Arn. and that high predator numbers contributed to lower recruitment and plant densities at lower elevations. The Forestdale Divide population is small and the high seed predation losses may be an important factor in limiting population size.

Yellow bellied marmots, pikas, Belding's ground squirrels, and alpine chipmunks were common around Frog Lakes until mid-September. Many marked *G. newberryi* flowers were removed by herbivores during August and corolla tubes were found on the ground with the base of the flower missing. During week four (September 5), there were only five *G. newberryi* flowers found at the site and many corolla tubes were found on the ground. It seems that flowers were removed as soon as they opened. The 38% of marked flowers removed by herbivores probably underestimates the impact of herbivores on seed production since flowers were removed before being marked for study. The following week (September 12), over 60 newly opened flowers were found but no marmots, grounds squirrels or chipmunks were detected. Of the flowers marked that week, only

one was removed. Marmots appeared to be the primary herbivores on *G. newberryi* flowers in the White Mountains, California (Spira 1983, Spira and Pollak 1986). Plants that flower after many of the herbivores begin hibernating reduce herbivore risk but are exposed to nightly freezing temperatures, occasional snowfall, fewer pollinators and risk snow cover before seeds have time to mature.

As a facultative self-compatible perennial, *G. newberryi* has numerous adaptations that allow populations to persist with different and unpredictable abiotic and biotic limitations. The late flowering period may reduce predation and competition for pollinators (Zimmerman 1980, Thomson 1981, Gross and Werner 1983) and when pollination is insufficient, self-pollination can produce viable self-fertilized seeds (Sutherland 1986, Barrett 1988, Barnes and Rust 1994). Vegetative reproduction requires less energy (Waller 1988) and new ramets can be produced when predators are removing flowers and seeds. The variance in predator pressure, pollinator availability, and ovule number result in different reproductive limitations among the sites. Resource differences can result in differences in flower size within and among populations. The amount and time of snowfall and other climatic factors vary among sites at different elevations and among years. Since factors influencing the reproductive output of a perennial species can be highly variable, it is important to document the variation within and among populations when trying to identify the adaptive value of observed life history traits.

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